

XXXVII.—*Subspecies and their part in Evolution.*

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MR. LOOMIS'S letter in 'The Ibis' (1920, p. 964) on subspecies contains many grains of sound commonsense, which, if it only makes us pause for a few moments to consider what subspecies really are, how they arise, and whither their recognition is leading us, will have had a most beneficial effect. It must be remembered—and the fact is too often forgotten—that nomenclature is a means to an end, and not the end itself. In order to be able to handle the vast array of facts presented by a study of Nature, naturalists have invented a system whereby relationships between various groups are roughly shown by methods of grouping and naming; and up to some 20 years ago the "species" was the smallest "item" in that system. The object of this system, however, was not merely to enable us to arrange our collections in cabinets, but that, having arranged them in some sort of a natural order, we might attempt with greater ease to unravel some of the mysteries of Nature's laws. I am not prepared to say that such a "unit" as a species actually exists in Nature. When it does it must have been brought about either because that species arose as a discontinuous variation, or because the connecting series of small variations have been lost so as to leave it without any obviously near relatives. This latter is the case, as we know, with many present-day species, and thus is formed what Mr. Loomis calls a "fundamental bird unit," although I do not agree with him that they are in any way "fundamental"; nevertheless, for practical purposes, they may be considered as "units."

Of late years the accumulating of larger and more carefully collected series has shown us that many of what were previously considered merely as sporadic varieties are in reality definite phases common to all individuals of a particular species in a certain area; and that such a form intergrades gradually into the form which happens to be next it geographically. These came to be recognized as

subspecies, and were designated in our "system" by a trinomial. In my own opinion the binomial species name is the only one that should appear as a heading in books and papers, and the subspecies should be given as a sub-heading—this, by the way, as my present object is not to deal with trivial details, but to get at what subspecies are and the part they play in evolution.

It is generally agreed, though the rule is frequently honoured in the breach, that trinomials should only be given to geographic forms—that is to say, to variations due solely to the influences of the climatic conditions of their habitat, and it is reasonably stretched to include island varieties; but it must not be forgotten that in an island race, "isolation" forms an additional factor which has influenced the separation; and in a closely-lying group of islands where each island has a distinct form though the climate is similar, "isolation" has probably been the chief factor in separating the race*. I will now consider Messrs. Lowe & Praed's letter ('Ibis,' p. 344), in which at the beginning they strike the right note by asking "of what scientific value are these variations?" I will not deal at length with the rest of this interesting letter, but merely note two points—they imply that subspecies are of two kinds: (1) due to "discontinuous" variation, (2) due to environment. I had always understood that a true subspecies was always supposed to be restricted to the latter cause, and certainly think it should be so. Secondly, they imply that variations (subspecies) caused by environment cannot be inherited; and hence it would follow that a true subspecies could have had no influence on evolution, and could never develop into a new species. Unfortunately, neither of these authors can have had any practical experience of breeding birds or animals, or they would realize how very small variations can be intensified and fixed from a purely selective, as apart from any creative, agency. They are quite right in carefully distinguishing between continuous and discontinuous variations, but they are

* The same conditions occur not unfrequently on land where races are separated by tracts of country unsuitable to them.

mistaken if they think that the latter alone influence heredity. In my book ('Vigour and Heredity,' p. 173 *et seq.*) I have gone more fully into the causes that may have brought about geographical races, but, put briefly, it amounts to this—changes of climate and food affect the "Vigour" (rate of metabolism) of an individual; externally this shows itself primarily in its colour, but also in many other ways. The climate acting through the general vigour of the individual will affect the nutritive value of the egg (*e. g.* underfeed a breeding bird and see if the chick is not a weakling), and thus the individual will tend to produce a progeny having a similar vigour to itself and also of a similar coloration.

I am not suggesting, of course, that such a change would take place at once, but only in the course of many generations; but none the less it does take place, and the conditions brought about by environment are inherited. A further proof of this is that when subspecies which have originated in different localities extend their range and meet in a common locality (*e. g.*, the Meadow-Starlings of North America*), they yet retain their subspecific characters. On this line of argument it is evident that discontinuous variations can never prove true subspecies, since they are not due to environment. Dimorphic forms may in some cases be due to environment; but these should, I think, be given specific rank, and, in any case, should not be regarded as subspecies and designated by trinomials, since they often occur side by side (*e. g.*, some Skuas, Herons, Fulmar, etc.). My conception of a species as a whole is that there are a number of "factors" which may or may not have a Mendelian inheritance, but which have a separate and definite inheritance. A "unit" species, say the Linnet, will contain a definite number of these factors; another nearly allied "unit" species, say the Redpoll, will contain a very large percentage of the same factors, but a few different ones, and so on. In dimorphic species—*e. g.*, Black-eared and Black-throated

* See Chapman, Bull. Amer. Mus. N. II. xiii. 1900, p. 318.

Wheatear, Blue and White Herons (*Ardea rufa*)—all the factors will be the same except one or two ; but on my reasoning they are none the less good species, because they do not contain *exactly* the same factors. Now all subspecies of a given “unit” contain exactly the same factors ; but the somatic expression of these factors has been originally altered by the environment, and subsequently become inherited. We have only to note in domestic types the reversion, after some generations, to the wild form to prove the truth that the factors have remained unchanged, but that the alterations caused by environment (domestication) have been so far inherited that the reversion is not complete for several generations.

Since the above was written, I have had the pleasure of reading Colonel Meinertzhagen's excellent article in the current number of 'The Ibis,' p. 528, to one or two points of which I should like to refer.

The author is of opinion that no deductions from mutations carried out on domestic varieties can be of value, since such conditions do not exist in Nature ; but surely by carrying out heredity experiments under conditions which we know, we are able the more accurately to attempt to understand the laws of heredity, and can then see if they would apply to wild species under natural conditions.

There is, to my way of thinking, no need to question whether species arose by mutations or by gradual selection. In the case of domestic freaks, which form but a small proportion of domestic races, they probably originated as mutations ; but by far the greater number of our “fancy” breeds to-day have been brought about by a process of careful and minute selection in order to intensify or diminish any particular trait or character ; and in that process each generation would show a larger and increasing proportion of individuals having that character, thus proving that not only any particular character, but also its intensification, was inherited. The reason this fact is not fully recognized is because of the comparatively short periods during which a

constant selection by one breeder, under the same conditions, is able to be carried out—say 25 to 50 generations at the most; and what is that compared with the ages which it has taken to develop species, or even subspecies? Facts on this subject being almost impossible to get, it is well to bear in mind a paper by Mr. H. Lyster Jameson (Journ. Linn. Soc., Zool. vol. xxvi. pp. 365–473) on a variety of a House-Mouse on a sand-bank in Dublin Bay, which sand-bank has only been in existence about 100 years; in this case the differentiation was only beginning and many normal coloured mice were found. In short, the question of time is all important, and to argue that nature proceeds on different lines from man because varieties produced by human agency easily revert, is fallacious if we compare the æons during which natural selection has acted, compared with the comparatively few generations during which artificial selection has been conducted. The fact, however, that variations artificially produced by man through an alteration of environment have been inherited for several generations when normal conditions were resumed, has been proved by Mr. W. E. Agar on variations in a Cladoceran (*Simocephalus vetulus*), and by Messrs. Delcourt & Guyenot on *Drosophila* (Proc. IV. Int. Congr. Genetics, Paris, 1913, p. 478); so that we have here considerable evidence that man's methods in producing new forms are not fundamentally different from those obtaining in nature.

Colonel Meinertzhagen wonders that no artificial variety of Fowl, Pigeon, or Canary has ever occurred in a wild state. This statement, if correct, would not be unexpected, since an artificial environment cannot occur in nature, and if such varieties did appear, they would show themselves in an initial stage and soon be swamped, whereas man has developed and intensified them by selection. In a wider sense, however, they do occur sporadically. For instance, a Canary—typically a green bird—is yellow in confinement, yet the nearly allied Serin shows a considerable tendency to yellow, and among Parrots (green birds) yellow varieties are

by no means unknown; or again, chequering, a character common to some domestic Pigeons but probably unknown in the pure wild Rock-Pigeon, is found in a few wild species of Pigeon—*e.g.* the Guinea Pigeon of Africa, and so on.

I am quite in agreement with Colonel Meinertzhagen that a mutation cannot establish a subspecies, since to my mind a subspecies is entirely an environmental or geographic form; and if my reasoning in the earlier part of this paper be correct, a geographic form could never become a separate species. It might, I conceive, be possible for some factor to become "latent" or lost through a change in the environment, and then a new species would evolve. Such an event might, by some, be termed a mutation (it would probably follow a Mendelian inheritance), but that is a debatable subject on which I will not venture at present.

Putting the above case on one side and omitting dimorphic forms which possibly fall in the above category, have we any definite knowledge of a new species originating as a mutation? Omitting *Pavo nigripennis*, which has not, I believe, occurred in a wild state, I can only recall the Italian Little Owl, *Athene chiaradia* (Giglioli, Ibis, 1903, p. 1); but unfortunately, although this sport was found in one or two places and seemed to be on the increase, it was collected for museums, and thus an unique chance of getting evidence on this problem was lost.

In putting forward these views, I do not claim that they are in any way indisputable or final, nor has it been my object to pour destructive criticism on the observations and thoughts of the previous writers; but they have been written in the hope that some of the energies now devoted to the naming of new forms may be diverted to consider why we have nomenclature at all, and whether it were not time that we made use of these subspecific bricks to add something to the existing structure of scientific ornithology.